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Ecological Considerations in Fisheries Management: When Does It Matter?

ABSTRACT

Ecological processes are often not explicitly included in fisheries models and management, but have the potential to be a significant influence on fish stocks. I examine cases from ecosystems around the world where predation, competition, environmental regime shifts, and habitat alteration have altered population dynamics, stock abundance, and community composition. These cases demonstrate the importance of ecological processes in the regulation of fish populations. Fisheries managers and scientists have long appreciated the importance of quantifying ecological processes relative to fishing, but recognizing the consequences of ignoring these considerations and developing a feasible set of widely used tools to implement these considerations has been lagging. Very simply, given what we know about the importance of these processes, particularly at low stock abundances, we would be wise to address them. I conclude with a proposed set of questions that need to be addressed in order to more widely and systematically implement ecological considerations in fisheries management.

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Introduction

Ecological processes are often not explicitly included in fisheries models and management, even though they have the potential to impact recovery of exploited stocks, surplus production, biomass partitioning, or biological reference points, and can be of the same magnitude as fishery exploitation. Multispecies, trophodynamic, and ecosystem considerations have a long history in fisheries science and are certainly not novel (e.g., Baird 1873; Lankester 1884; Lotka 1925; Volterra 1926). Several approaches were developed in the 1970s and 1980s to extend single species models by incorporating some of these broader considerations in a fisheries management context (Steele 1974; Andersen and Ursin 1977; May et al. 1979; Mercer 1982; Kerr and Ryder 1989; Daan and Sissenwine 1991). Additionally, there has been considerable recent interest in ecosystem approaches to fisheries management (e.g., Christensen et al. 1996; Larkin 1996; Jennings and Kaiser 1998; NRC 1999). Yet the implementation of broader ecological considerations has not become widespread in fisheries management even though it has been emphatically advocated (NMFS 1999; NRC 1999) and mandated (NOAA 1996).

For scientific, institutional, philosophical, or logistical reasons, ecological factors are often omitted in fishery management. In some cases this is justifiable, but in many other cases omitting ecological considerations is imprudent. Recognizing the importance of ecological processes in the regulation of fish populations is a key step to a broader approach of fisheries management. Given that over 70% of global fisheries are fully or over-exploited (NRC 1999) and that fishing pressure will (by economics, regulation, or legislation) be lessened on these stocks, it is likely that ecological factors will be increasingly important for these fish. I examine cases where predation, competition, environmental regime shifts, and habitat effects have influenced stock dynamics and consider how we can better incorporate ecological processes into fisheries management.

Predation

In spite of the importance of predator-prey interactions in fisheries systems (Bax 1991, 1998; Carpenter et al. 1985; Christensen 1996), there is little evidence that predation causes large, persistent stock declines. However, when a stock is already depressed and in the recovery phase, there is no question that predation may be the leading factor limiting or capping a strong year class and subsequent recruitment (Sissenwine 1984; Bax 1991, 1998; Christensen 1996). Additionally, the resurgence of a predator population after a release of fishing pressure may have a strong impact on depressed or highly susceptible prey populations (Carpenter and Kitchell 1993).

The trophic cascade work in lakes provides well documented examples of how predators can control populations of fish at lower trophic levels (Carpenter et al. 1985; McQueen et al. 1986; Carpenter and Kitchell 1993). The addition of largemouth bass (*Micropterus salmoides*), a top piscivore, to Tuesday Lake, reduced minnow population levels (Carpenter and Kitchell 1988). Generally, but not without complications, minnows increased in abundance following the removal of largemouth bass in a reciprocal lake, Peter Lake. Fishing pressure on upper and mid-trophic level fishes such as these bass can significantly alter energy flow and biomass at lower trophic levels in lake ecosystems.

Predation by piscivorous birds such as cormorants has been suspected to be a major detriment to recovering or depleted fish stocks. Lake trout (*Salvelinus namaycush*) in Lake Ontario (MacNeill 1994; Neuman et al. 1997), grayling and trout (salmonids) in Switzerland (Staub et al. 1998; Suter 1998), yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) in Lake Oneida (L. Rudstam, Cornell Univ., pers. comm.), and flatfish (Pleuronectiformes) in the Wadden Sea (Leopold et al. 1998) are examples where this bird has negatively impacted fish populations. In some cases, predator control methods have been implemented to reduce the impact of cormorant predation.

Predation is strong for many marine pelagic fishes. In these cases natural mortality is often the larger proportion of total mortality due to the ubiquity of predators on these organisms and typically low fishing pressures (e.g., Beddington et al. 1985; Overholtz et al. 1991; ICES 1994; Overholtz et al. 2000). However, this may change as more and more fisheries target these forage fish at lower trophic levels (Pauly et al. 1998). Unlike lakes and more closed systems, it is also unclear whether predators can control populations of marine pelagic species (Jennings and Kaiser 1998). When population abundances of herring (*Clupea harengus*) were low in the northwest Atlantic, most predators switched to other pelagic species (e.g., Overholtz et al. 1991; Overholtz et al. 2000). Once fishing pressure was reduced on herring, the stock recovered to record levels while predators ate mackerel and sand lance. Now, herring again dominate the pelagic component of the ecosystem due to a release in fishing pressure and subsequently also dominate the diet of piscivorous fish.

Competition

The main requirement for demonstrating interspecific competition is limiting resources. In many lacustrine and marine systems, particularly coastal and continental shelves, productivity is generally high (Sherman 1991; Sherman et al. 1993), and total production, coupled with the opportunistic generalist nature of most fishes (Hartley 1948; Gerking 1994), suggests that this phenomena is not common in most fishery systems. The exceptions are smaller, more closed ecosystems or ecosystems with a high number of specialist species.

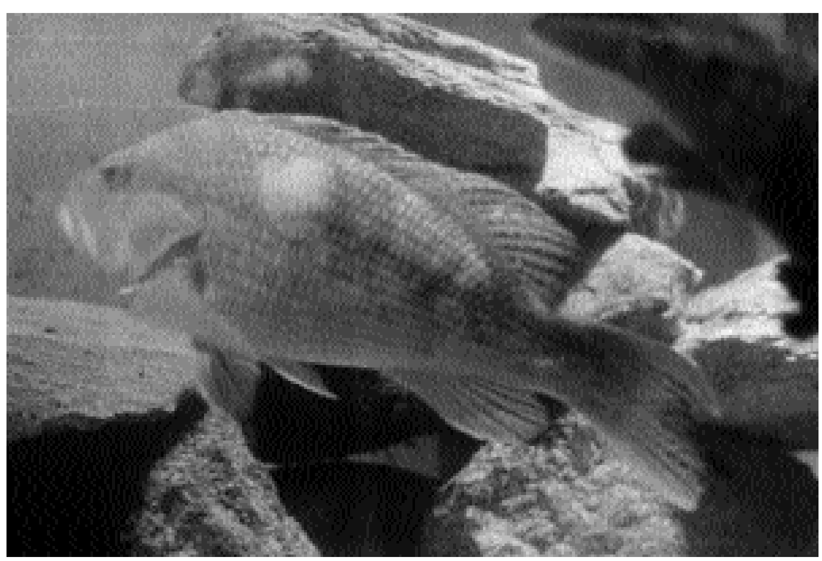
An example where competition is a key factor in determining species abundance is coral reefs. Hourigan et al. (1989) have demonstrated the importance of defending feeding territories for various angelfish in the Caribbean, where these species drive off other species. This antagonistic behavior effectively limits those competitors to inferior habitats, with the implication that this competition for space limits the population abundance of other fish species. Other researchers similarly have observed strong resource partitioning in reef systems, which could be as or more important than fishing pressure in determining species abundance (e.g., Montgomery 1980; Klumpp and Polunin 1989). There are clearly observed changes in reef fish, benthic, and algal communities that have been attributed to fishing, ultimately altering the competitive balance and associated trophic structure among these communities (McLanahan 1992, 1994; Jennings and Polunin 1996, 1997).

Lakes and ponds also exemplify competition among fishes, where trophic interactions dominate habitat choice, survivability, and abundance among different species. Examples of various centrarchids selecting habitats based upon food availability, the ability to outcompete con-specifics, and to avoid predators are well documented (e.g., Mittlebach 1988; Werner et al. 1983). Release of fishing pressure often elicits top-down effects, intensifying competition among fish at trophic levels that were previously regulated via predation (Carpenter et al. 1985; Carpenter and Kitchell 1993).

Environmental Regime Shifts

Walters and Collie (1988) discuss the challenges and pitfalls of including environmental variables in fisheries models, and how these variables can confound the particular issues of distribution and recruitment. For instance, some species live long enough to effectively integrate changes in abiotic factors, whereas other species are heavily exploited and their response to abiotic factors is masked by the magnitude of fishing effects. The challenge has been to clearly demonstrate cases where abiotic factors have significantly influenced habitat usage, species distribution, and population abundance.

Salmon in the north Pacific are an excellent example where changing environmental conditions have influenced stock abundances, with these populations exhibiting oscillations related to the Aleutian



Black sea bass in a Woods Hole aquarium.

Low Pressure Index (Beamish 1993; Beamish and Bouillon 1993; Beamish et al. 1999). An increase in the abundance and catch of several salmon (and other) species coincided with a regime shift in atmospheric conditions. It is contentious whether the increases in salmon catch were entirely due to this regime shift or freshwater life-history considerations, but the magnitude of increase in salmon production in the 1970s was largely unexpected, driven by some kind of environmental factors, and could not have been predicted by single species models. Francis et al. (1998) and Hollowed and Wooster (1995) describe a similar pattern for other fish in this region.

In the Gulf of Guinea, shifts in the catch of *Sardinella* were attributed to both temperature changes (which again lead to changes in food availability) and differential fishing pressures (Binet and Marchal 1993). Partitioning the variance between the two causes remains a daunting challenge, but dominate the choice of possible explanations. Additionally, ignoring the possibility that the fish may have simply migrated differently (earlier, further offshore, etc.) in response to different oceanic conditions instead of assuming they were removed by neighboring nations with higher fishing effort is not diplomatic. Environmental considerations have been widely recognized as one of the more important considerations when assessing fish that inhabit similar upwelling ecosystems (Sherman 1991; Sherman et al. 1993).

Sinclair (1996) has hypothesized that as fishing on Atlantic cod (*Gadus morhua*) ceased in Canadian waters, the North Atlantic Oscillation may have become an increasingly important influence on cod stocks. He reviewed the abundance of cod stocks, fishing, and environmental variability and concluded that there is evidence that cod recruitment is strongly related to broadscale environmental factors that change in magnitude and impact.

Habitat Alteration

There has been much recent interest in the effects of fishing on habitat and non-target species, and how these effects can regulate populations of commercially valuable species (e.g., Jennings and Kaiser 1998; Benaka 1999; Kaiser and de Groot 2000). The general paradigm is that as habitat complexity increases, sensitivity to fishing effects increases (Auster and Langton 1999). Fishing pressure usually supercedes ecological processes, and causes a notable decline in benthic megafuana and habitat complexity (Jennings and Polunin 1996; Collie et al. 1997; Auster and Langton 1999). If fishing is stopped but there is no habitat or benthic food for juvenile settlement, development, or survival, it is unclear whether populations will recover or remain depleted.

Coral reefs provide excellent examples where changes in habitat influence population abundance. Sainsbury (1988) and colleagues (Sainsbury et al. 1997) demonstrated that when biogenic benthic habitat of the northwest Australia shelf was reduced due to the effects of fishing gear, densities of commercially valuable lutjanid and lethrinid species similarly declined. In areas given time to redevelop adequate biogenic habitat or that were protected from fishing altogether, these species were significantly more abundant.

Seagrass habitats are an example where changes in habitat alter the effectiveness of spawning and nursing grounds for many fish. Seagrass habitats are particularly susceptible to impacts from fishing gear (Fonseca et al. 1984). Higher species abundance, diversity, production, and recruitment have been strongly correlated to the presence and extent of seagrass habitats in many estuaries (Heck and Orth 1980; Orth et al. 1984; Connolly 1994). Although confounded with other factors (e.g., eutrophication, hypoxia, harmful algal blooms, etc.) reductions in seagrass biomass from fishing gear have led to subsequent declines in species abundance, diversity, and recruitment (e.g., Short et al. 1986, 1995; Peterson et al. 1987; Valiela et al. 1992).

There has also been a clear effect of fishing on the benthic habitat of the Gulf of Maine-Georges Bank ecosystem in the northwest Atlantic. In addition to acute effects on fish stocks, reductions in biogenic structures, habitat complexity, infauna biomass, and benthic community diversity have been documented in heavily fished or dredged areas (Auster et al. 1996; Collie et al. 1997). Many of the benthic species impacted are important prey items for cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), yellowtail flounder (*Limanda ferruginea*), and other commercially valuable species (Garrison and Link 2000). Additionally, the mortality of juvenile cod declines with increased habitat complexity (Lindholm et al. 1999). Recent work with Georges Bank marine protected areas have demonstrated that after 3–5 years of closure, populations of haddock and yellowtail flounder are beginning to recover (Brown et al. 1998). Similar patterns have been observed in European waters (Kaiser and de Groot 2000).

Simultaneous Processes- Implications for Recovery

Simply presuming that ceasing exploitation on an overfished stock will result in stock recovery ignores the uncertainty imposed by ecological processes, yet many of our fisheries models and texts implicitly, and often explicitly, assume stock recovery to be a given if fishing effort is reduced. Realistically, other than small, closed systems, we have very few instances where fishing pressure has been relaxed to the magnitude for us to see the complete recovery process. It is highly likely, however, that with over 70% of the world's fish stocks fully or over-exploited (NRC 1999) we will have more cases where fishing will have to stop (either directly by management or indirectly via economic infeasibility), providing us the opportunity to examine the potential for stock recovery. In a recent review, Hutchings (2000) demonstrated very little evidence of recovery for 90 marine fish stocks, even if one assumes there has been no shift to alternate equilibria in these ecosystems.

An example of a recovering fishery is lake trout (*Salvelinus namaycush*) in Lake Superior and Lake Huron (Eshenroder et al. 1995; Hansen et al. 1995; Selgeby et al. 1995). This species exhibits signs of restoration in these upper Great Lakes in spite of the introduction of exotic, competing species, a shift in prey base, eutrophication, toxic depositition, and a voracious ectoparasite. A good example where releasing fishing pressure on a stock has not worked is lake trout in Lake Erie and Lake Michigan (Cornelius et al. 1995; Holey et al. 1995; Selgeby et al. 1995). Lake trout face many of the same obstacles as in Lakes Huron and Superior, yet the impacts of eutrophication, differences in spawning habitat availability, and a slightly different community composition have had a greater effect in limiting the recovery of this species in these lower lakes. The Great Lakes example is particularly germane as it demonstrates the different responses of similar and relatively simple ecosystems to similar management strategies.

Discussion

The examples above demonstrate the significance of ecological processes on commercially valuable fisheries. Even in cases when causality has not been explicitly partitioned between fishing activities and ecological processes, the latter are a notable and logical consideration when examining the factors that influence fish stocks. Obviously I have not treated any of these four topics in the depth that they require—each one has been the subject of numerous reviews, books, and symposia. However, the limited examples presented highlight the importance and the ubiquity of these processes in a variety of ecosystems.

I am not suggesting that all fisheries scientists quit their jobs and become community ecologists, oceanographers, benthic biologists, or the like. Nor am I suggesting that all single species approaches be dropped. Rather we need to recognize the value of multi-disciplinary considerations along the gradient from population to entire ecosystem approaches (Figure 1 of Link 2002, this issue). Murawski (2000) reviewed several single species approaches that incorporated broader ecological processes and subsequently provided improved results over classical single species models. We can and should continue to incorporate these approaches.

Additionally there are other approaches along the gradient (Figure 1 of Link 2002, this issue) worthy of further development and implementation that focus on multispecies, aggregate biomass, or entire systems that have not been widely utilized and are potentially useful tools. Several models have shown some promise in at least qualitatively predicting multispecies trajectories (e.g., Walters et al. 1997; Hollowed et al. 2000; Whipple et al. 2000). Given the complexity of most ecosystems, the issue of predictability will, however, remain. Yet even if we can at least qualitatively predict or index "the climate, and not necessarily the weather," we will have made substantial improvement in incorporating ecosystem approaches into fisheries management and use of the insights that these approaches can provide.

The question remains, if ecological processes have the potential to significantly influence fish stocks, why aren't these considerations incorporated into fisheries management more broadly and systematically? I submit there are six reasons. First are logistical concerns related to the data availability and collection required to address ecological considerations. Second are limited resources (time, money, and staff) of resource management agencies. Third are concerns that using ecological and more holistic approaches will serve as an excuse not to implement clear-cut single species advice. Fourth are philosophical disagreements in fisheries science on the importance of "lower tier" processes (sensu Schaeffer 1956). Fifth, as a reviewer of an earlier version of this manuscript pointed out, is the fear that including ecological considerations may increase complexity and thereby add further uncertainty into the management process. Finally, there is the perception that we don't know how to actually do it. Even if one recognizes the importance of ecological processes and how they influence stock dynamics, has abundant and appropriate data, and has an institution willing to support this type of an approach, given the present state of our knowledge, how can we operationally and systematically incorporate ecological processes into fisheries management?

Allow me to propose a series of questions to address how we can begin to systematically implement ecological processes more explicitly in fisheries management. Recognizing that these processes have been important in some ecosystems causes us to ask if they are of similar importance in other ecosystems under consideration.

A Checklist for Ecological Issues in Fisheries Management

The examples presented in Table 1 demonstrate that the characteristics of a particular ecosystem and set of species determine the relative importance of trophic interactions, abiotic factors, and fishing mor-

Table 1. A general list of issues that need to be considered for implementing ecological considerations into fisheries management.

Geography of the Ecosystem

- What are the key features of the ecosystem under consideration? For example, is the system relatively open (e.g., mid-sea, continental shelf) or closed (e.g,. river, small lake).
- How big is the ecosystem?
- What are the important, dominant, and unusual physio-chemical factors in a system?
- Is there a prominent geologic, bathymetric, or similar feature that defines and dominates the system?
- What are the political boundaries and jurisdictions that govern the resources in a system?
- How dense is the human population in or near the ecosystem?

Key Species

- What are the key species in the ecosystem? Certainly a list of commercially exploited species is required, but non-commercial yet ecologically valuable species should also be included.
- What are the key aspects of these species?
- Are the species involved relatively slow growing with a long life-span, or are they more r-selected?
- What is the size of the species in the system?
- What is the extent or range of the species of interest in a system? How are they spatially distributed?
- How economically valuable are the exploitable species?
- Are there any keystone species? Are there any dominant species?
- What is the functional role of the key species?
- Have the life history parameters for a species changed over time-e.g., faster growth, earlier age-at-maturity, etc.? Have they even been determined?
- Are there any species that are particularly susceptible to an ecological process?
- Are there any specialists?
- Are there any species that are near extinction?
- Are there any species that have an excessively high linkage density (i.e., high number of predators or competitors)?
- Are there any species that have sensitive or low-output reproduction?

Abiotic Factors

- Are there certain spawning or nursery grounds that merit protection?
- Is there a particular habitat feature such as stacked cobble or sea grass or oyster beds that enhance the survivability of juvenile fish?
- Is there a particular area that is optimal for growth?
- What are the distinguishing paramaters of the physio-chemical environment?
- Are there particular features such as a thermocline or frontal boundary that aggregate prey for fish feeding?
- Has the habitat been altered in any way?
- Are there any toxins in the system that can kill or chronically impair a species?
- Is the system susceptible to large scale perturbations such as an hurricane?
- Is there the possibility that an hypoxic zone could develop?
- Are other forms of pollution prevalent and significant?
- Could harmful algal blooms develop, and what effect would they have on key species?
- Is there evidence of a long-term regime shift in temperature, atmospheric pressure, upwelling, or similar meterological factors? Have circulation and current patterns changed across time?
- How strong are tidal influences? Have they changed?
- Are certain life stages or certain species particularly susceptible to environmental change?

Species Interactions

- Have the interactions between species been established? If so, can they be quantified?
- What is the amount of food required to maintain a predator population at a certain size structure and abundance?
- What is the total number of individuals or biomass removed by all predators of a particular species?
- Is there evidence of prey switching?
- Are the interactions between species strong and tightly coupled, or is it a system of generalists with weak species interactions?
- Is there one species that is clearly a competitive dominant?
- Is there evidence of dietary, spatial, or other resource overlap?
- Is there an indication that resources may be limiting?
- What are the key resources in a system for fish, plankton, benthos, etc.?
- Is there a potential for conflict among fisheries targeting different species?
- Are there management protocols in place to objectively resolve these conflicts?

Aggregate Properties

- What is the productivity of the ecosystem? Has it changed across the life span of key species? How does this affect carrying capacity for upper trophic levels?
- Similarly, have there been changes in secondary production in the system?
- Is an understanding of the dynamics of lower trophic levels such as benthos or zooplankton essential for the key fisheries?
- Is the food web tightly connected to the nutrient dynamics of a system such as an estuary or small lake?
- Are there significant guilds in the system?
- How is the energy and biomass of the ecosystem partitioned amongst different functional or aggregate groups?
- What is the dominant group?
- Has this group remained dominant across time? If not, what caused the changes?

System Level Properties

- Are there other ecosystem goods and services that compete with a fishery or a particular species? Conversely, are there synergisms between different user sectors?
- How does a fishery interact with other sectors that use an ecosystem, for instance tourism?
- Are there protocols to address these potential conflicts or encourage possible collaborations?

The Fisheries Context

- What type of fisheries have been in the system—commercial, recreational, artisinal, etc.?
- What type of gear has been and is being used?
- What has been the historical level of fishing effort on key species in the system?
- What is the current level of fishing on key species in the system? How does this influence non-target species, trophic structure, habitat, etc.?
- What are current landings and discards?
- Can we adapt gear or target species as a group that have high technological interactions?
- Where are stocks relative to historical levels of abundance—declining, collapsed, or recovering?

tality. No standard set of conditions and rules applies to all ecosystems, and attempting to prescribe a common set of goal functions for each ecosystem is imprudent. I won't presume to advocate any particular methodology or model, rather a general list of issues that need to be considered for implementing ecological issues in fisheries management (Table 1). Answers to these and similar questions will help determine the more important factors in any given system.

How can one use answers to questions proposed in Table 1 as fisheries management advice? The first way is triage. Determining which is the most important process in an ecosystem is valuable and should not be discounted. Knowing the magnitude, and hence which are most important, of the major processes in an ecosystem is not trivial. Second, answers to these questions could be used to quantitatively modify existing fisheries management advice. For example, the International Commission for the Northwest Atlantic Fisheries (ICNAF) used two-tier quotas that set limits on single-species as well as aggregate biomass removals from the northwest Atlantic (Brown et al. 1976). In this vein, one could set aside a prescribed amount of a harvested forage fish to ensure adequate food for protected species or predators that are also commercially harvested. Finally, answers to these questions could be used to qualitatively modify the direction of fisheries management advice. For example, if an environmental regime shift has occurred or available habitat has increased, one would expect that carrying capacity or production rates for some species could be modified (up or down) based upon the new conditions.

Conclusion

To incorporate ecological considerations into fisheries management, we do not need a radical, rapid change in thought and methodology. We do not need to answer every one of the questions listed in Table 1 to even begin. We do not need to ever have a full and complete understanding of ecological processes. However, we do need an investment in the data required to elucidate the magnitude of ecological processes. We do need to expand multispecies, trophodynamic and ecosystem modeling and monitoring. We do need an explicit recognition that ecological processes can have significant influence on fish stocks.

The Ecosystems Principles Advisory Panel (NMFS 1999) advocates inclusion of ecological processes for more holistic fishery management. I submit that to formally begin to do this, the questions listed in Table 1 should serve as a useful start. I also assert that addressing even a few of these issues is very feasible and can improve our management advice and scientific understanding. Given the increasingly multi-user interests, allocation demands, and shrinking amounts of fisheries resources, we need to begin formulating advice that incorporates these ecological processes.

The challenge remains to quantify the magnitude of ecological processes relative to fishing. Fisheries managers and scientists have long appreciated the importance of addressing this challenge, but recognizing the consequences of ignoring ecological considerations and developing a feasible set of widely used tools to implement these considerations has been lagging. In the end, how do institutions that are already spread too thin commit resources to address these broader issues? Very simply, knowing what we do about the importance of these processes, particularly how they can influence stocks at low abundances, it would be wise to begin to do so.

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